The Problem of Utility: Are Specific Characters always or generally Useful? By Alfred R. Wallace, LL.D., F.R.S., F.L.S.

[Read 18th June, 1896.]

The above stated question is discussed at great length in the second part of the late Mr. Romanes' work on 'Darwin and After Darwin,' fully half of the volume being devoted to it; and in the preface the author states his belief that his arguments are so conclusive that he has "broken to fragments" the doctrine of utility, and that he has "made a full end thereof." A careful perusal of the volume, and a full consideration of all the facts and arguments adduced therein, seem to me to leave the problem just where it was before; but the variety of the subjects discussed, the great mass of details referred to, and the ingenuity of some of the arguments in support of the author's view, lead me to think that I have not hitherto set forth the facts and arguments in favour of the utility-theory with sufficient completeness, while I am indebted to the lamented author for pointing out one or two weak points in my discussion of the question, and for a number of useful references to Darwin's statements on the points at issue, some of which I had overlooked. Although Mr. Romanes' discussion of the question is so lengthy, the problem itself is in its essence a comparatively simple one, and is I believe capable of being solved by a reference to well-known facts and admitted principles. The reason why Mr. Romanes is able to support his views by so many quotations from Darwin's works, is due to the fact that Darwin was firmly convinced of the heredity of acquired characters, and especially of the influence of food and climate and the effects of use and disuse; and this belief must be borne in mind whenever he speaks of specific characters being due to other causes than natural selection. It must also be remembered that Darwin was not acquainted with the evidence we now possess as to the extreme frequency of variation everywhere in nature, its large amount, and its universality in every organ and every character that can be measured or otherwise estimated. Had he known what we now know on this subject, he would not so frequently have made the proviso—"if they vary, for without variation natural selection can do nothing," or have alluded to the possibility of variations of the same kind occurring "perhaps after a long interval of

time." We now know that variations of almost every conceivable kind occur, in all the more abundant species, in every generation, and that the material for natural selection to work upon is never wanting. Accepting, then, these facts of variation, and always keeping in mind the severity of the struggle for existence, nine tenths at least of the progeny of the higher animals perishing annually before reaching maturity, thus leading to a systematic and continual weeding out of the less fit—let us endeavour to realize the process of the formation of new species and the nature of the characters which distinguish allied species from each other.

In my article on "Mimicry and other Protective Resemblances among Animals," first published in 1867, I laid down the principle of utility, perhaps a little too absolutely, in the following passage:—"Perhaps no principle has ever been announced so fertile in results as that which Mr. Darwin so earnestly impresses upon us, and which is indeed a necessary deduction from the theory of Natural Selection, namely—that none of the definite facts of organic nature, no special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species, can exist but which must now be or once have been *useful* to the individuals or races which possess them." Professor Huxley, in his obituary notice of Darwin, expressed the same idea as follows:—"Every variety which is selected into a species is favoured and preserved in consequence of being, in some one or more respects, better adapted to its surroundings than its rivals. . . . . For, as has been pointed out, it is a necessary consequence of the theory of Selection that every species must have some one or more structural or functional peculiarities, in virtue of the advantage conferred by which it has fought through the crowd of its competitors and achieved a certain duration. In this sense it is true that every species has been 'originated by selection.'" Now these characters, in virtue of which the variety has become a species, are in fact its "specific characters," and they alone will absolutely differentiate it from all other species. We need not trouble ourselves about the cases of doubtful species, in which the distinctive characters are either so minute or so unstable that we cannot invariably determine them. On the theory of evolution by natural selection there must be such cases. They are species in the making and not

quite completed. But in the great majority of species definite characters do exist by which any single individual can be recognized and the species to which it belongs be determined; and the question is, whether or no the characters, or combination of characters, which thus differentiate it are now useful or were useful at the time of its origination*. In order to answer this question, we must briefly summarize both the facts and the admitted principles or theories which bear upon it.

Every extensive area contains a number of large and dominant species which appear to be, and probably are for considerable periods, stable, both in average population and in the extent of the area they occupy. Taking any one of these species—say of bird or mammal—so long as the whole conditions of its environment remain unchanged or very little changed it will, theoretically, continue to maintain itself, as we know many species have maintained themselves during the whole period since the glacial epoch, and some very much longer. The species, however, is not absolutely homogeneous. It varies in every generation, not minutely or infinitesimally as was formerly supposed, but very considerably, the variations being easily seen and measured by any one who looks for them; and they extend, so far as we know, to every part of the organism, external and internal, since no part has yet been found to be invariable when a large number of individuals have been compared. The species is therefore composed of a fluctuating mass of variable units which yet maintain the same general average of characters, and this it can only do by a constant or intermittent weeding out of the extremes in every direction. Such a weeding out on a large scale takes place annually, because, although the annual increase by birth is very large, the population of adults remains approximately fixed. The species is maintained in harmony with its environment by the survival of the fittest.

But now let some important change occur, either in climate, in abundance of food, or by the irruption of some new and hitherto unknown enemies, a change which at first injuriously

* To this should be added—"or were correlated with some useful characters." I have referred to such correlations in my 'Natural Selection and Tropical Nature,' pp. 172 and 175; and as to apparently useless characters being in some cases correlated with those which are useful, in my 'Darwinism,' p. 140; but it is cumbersome to restate this part of the theory whenever it is stated that all specific characters are useful.

affects the species. It must, therefore, undergo some amount of modification, either structural or functional, in order to succeed under the new conditions; and the constant variations of every part around its mean furnish the materials for adapting the organism to these new conditions. If a new enemy is the danger to be guarded against, this adaptation may be effected in several ways. Swiftness in running or flying, habits of concealment, or seeking new kinds of food in places inacessible to the enemy, may each lead to the survival of those individuals which were sufficiently intelligent to adopt them or sufficiently favoured by rapid variation in the desired direction. Survival of the fittest in these respects, going on year by year, might lead to the formation of two or more diverging races each able to maintain itself in the presence of the new enemy, while the former average type of the species rapidly became extinct. We should thus have two or three incipient new species; but they would not become well differentiated species till they had acquired certain definite and important characteristics. These are (1) some amount of infertility when crossed with the parent form or with each other; and (2) some distinct and conspicuous external characters by means of which the new varieties could readily distinguish their own kind even when at considerable distances or when partially concealed; or, in the case of flowering plants, be distinguished by the insects which fertilize them.

The greatest danger to a species under new and adverse conditions is, that it should not be able to adapt itself to them with sufficient rapidity. It is for this reason that, as Darwin concludes, new species arise, mainly, from those which have a large population, which occupy a wide area, and which present much variation—a combination rarely found except in continental areas. But this danger is evidently much increased if crossing with the parent form is not at first checked and soon afterwards completely prevented, except as a quite exceptional occurrence. The means of preventing this intercrossing are, for animals, either infertility, external distinctions leading to the preferential mating of similar forms, or physical isolation. The latter I believe, with Darwin, to be of comparatively little importance and to have very rarely been the chief agent in modification. In the great majority of cases a new species must arise amidst the population of an existing species; and while its adaptation is progressing any intercrossing with the parent form will be

injurious. I have endeavoured to show, and can still find no flaw in my reasoning, that mutual infertility would be usually brought about by natural selection wherever the two forms were in contact, and also that the early occurrence of well-marked external differences would assist greatly in the rapidity of adaptation *. This view will explain the curious fact of the well-marked differences of colour or form which almost invariably characterize allied species. These "recognition marks," as I have termed them, are of great use even to existing well-defined species, but they must have been of still greater use during the earlier stages of differentiation, when the very existence of the new form must have largely depended on them.

I may here remark that it is because these external differences of colour or marking are quite as constantly present in peculiar insular species as in those inhabiting a continent, that I do not believe in local isolation as of any importance in species-formation. Insular species may have been produced in two ways. Either a portion of a declining species may have reached the island, where it survived through the more favourable conditions while it became extinct on the continent; or, a few individuals of a dominant species reached the island, where, owing to the absence of competition, they rapidly increased till the island became fully stocked with the unchanged species. Then (and then only) survival of the fittest would begin to act, and the differences of food and climate, with the different kinds of enemies, would render some modifications of structure, form, or colour advantageous, and thus a new species would be formed by adaptation from the old one in almost exactly the same way as on the continent. In both these cases recognition-characters, to aid in the prevention of intercrossing, would be produced by natural selection. But if insular species have usually been formed by a few individuals somewhat different from the type having first reached the island and thereafter preserved their peculiarities, there is no reason why any distinctive and stable form of coloration or marking should have been developed, since there would be no similar species from which it would need to be differentiated. Neither is the small amount of divergence that usually prevails between the mean of a few individuals taken at random, such as might have accidentally reached an island, and the average type

* 'Darwinism,' pp. 174-180.

of the species, at all comparable with the well-marked characters that usually distinguish insular forms, and there is nothing in mere isolation without selection which can increase the difference. As examples we may refer to the many peculiar species of butterflies and birds found in the various islands of the West Indian and Malayan Archipelagoes, which are quite as distinct from each other as are allied continental species, and which exhibit all the characteristics of forms which have been fully differentiated by natural selection.

The sketch now given of the usual mode of formation of new species under natural selection leads to the conclusion that every species (of the higher animals at all events) will usually possess at least three peculiarities: in the first place, it must exhibit some difference of structure or function adapting it to new conditions; secondly, some distinction of colour, form, or peculiar ornament serving as distinctive recognition marks; and, thirdly, the physiological peculiarity of some amount of infertility when crossed with allied species. The first two constitute its "specific characters." But if we consider that every species in the long line of its ancestry must have had similar specific characters, adapting it to the peculiar conditions of its environment and distinguishing it from its nearest allies; that some of these characters, when generally useful, have persisted, and now constitute generic or family characters; that others have been again and again modified so as to adapt them to new and sometimes quite different conditions; and that others again, becoming useless, persist when quite harmless or remain in a more or less rudimentary condition; and when we further consider that many genera and families extend far back into geological time and must have originated in the midst of a physical and biological environment very different from that which now prevails, we shall dimly understand how complex are the forces and processes which have led to the assemblage of characters now presented by each organism, and how difficult it must be to determine positively that any one of these characters is not, *nor ever has been*, useful to its possessor. Yet this is what is done by those writers who maintain, as did the late Mr. Romanes, that the majority of specific characters are not and never have been useful, but have arisen through definite variation under the influence of definite causes, and, when neither useful nor hurtful, persist and constitute the main external differences which we observe between

species and species. This theory, which, although to some extent held by Darwin himself, I consider to be wholly erroneous, we will now proceed to discuss.

It may be well first to dispose of a point, made much of by Mr. Romanes, that I do not urge utility as a characteristic either of varieties or of genera and higher groups, and that it is therefore illogical to claim it for species. But this is a misapprehension, since I *do* claim that when varieties are constant, are hereditary, and occupy a definite area, and are therefore what Darwin termed "incipient species," the characteristics which distinguish them from the parent species are, to some extent, adaptive and useful, and will become fully so when the variety becomes a fully differentiated species. And as to genera and families, it is obvious that every one of their distinguishing characters was once a specific character, since genera are merely groups of species, all of which were derived from one parent species, and which have become more or less isolated by the extinction of intermediate forms. Families are, in the same way, derived from a single genus and ultimately from a single species, and the same reasoning applies to them. The reason why my argument on this question has been limited to species is, because the whole problem is included in that of species: it is in them that the process and laws of development can be best studied free from many of those complexities of modification and survival of disused and partially aborted parts and organs which often constitute generic or family characters. If every one of the new characters or new combinations of characters which arise when a new species becomes differentiated from its parent-form,—if every one of these is adaptive and utilitarian, then no higher groups can possess characters other than those which were once adaptive, since genera and families can never acquire new characters except through every one of their component species acquiring those characters. The problem as exhibited in species includes therefore the problem in all higher groups.

I have already set forth in some detail the argument for utility founded on the fact of the continuous progress of the discovery of utilities with the continuous growth of our knowledge of the life-histories and inter-relations of plants and animals *. I will therefore now devote more special attention to the fundamental argument, that whereas every modification of a species which

* 'Darwinism,' pp. 131–142.

arises under the influence of natural selection must, from the very nature of its origin, be useful to the new form, no other agency has been shown to exist capable of producing non-utilitarian characters *in every individual constituting a species, neither more nor less.* Now the general cause which is adduced as being able to do this is stated by Darwin in the following passages, which are quoted by Mr. Romanes as expressing his own views :—

" There must be some efficient cause for each slight individual difference, as well as for more strongly marked variations which occasionally arise ; and if the unknown cause were to act persistently, it is almost certain that *all* the individuals of the species would be similarly modified " (' Origin of Species,' p. 171).

Again, after referring to cleistogamic flowers and degraded parasitic animals, he says :—

" We are ignorant of the exciting cause of the above specified modifications ; but if the unknown cause were to act almost uniformly for a length of time, we may infer that the result would be almost uniform ; and in this case all the individuals of the species would be modified in the same manner " (' Origin,' p. 175)*.

Now these passages, merely as stating a possibility or a probability, appear to me to be wanting both as regards logic and in the absence of any appeal to the actual facts of variation. For the argument is, briefly, that the same causes will always produce the same or closely similar results. But this is only true when the same causes *act upon identical materials and under identical conditions.* But the very foundation of the Darwinian theory is, that the materials—the individuals of a species—are *not* identical, but that they vary indefinitely and in many directions even under closely similar conditions. How then can any external or internal causes produce an identical result—a definite new variation—in *all* the individuals of a species, born as they are of varying parents, of different ages, and subject to ever fluctuating conditions ? It seems to me, therefore, that the *à priori* probabilities are all against Darwin's supposition.

Now let us see how far the *facts* of variation give any support to the theory of useless specific characters. If there is one thing better established than another it is that the individual variations which are constantly occurring in all common species

* In my ' Darwinism,' p. 141, I have stated my opinion that Darwin did not believe in the production of useless characters in *all* the individuals of a species. I had overlooked the passages quoted by Mr. Romanes and given above, which certainly show that he did believe it.

are indefinite in their character and very unequal in their amount. Some species are much more variable than others, and Darwin has shown reasons for believing that any change of conditions induces *variability*, but not that it causes definite *variations*. The two things are radically distinct. So far as I am aware, no evidence has been adduced of any special conditions which have produced a definite variation in the whole offspring of all the individuals subjected to it. But it must do more than this. For it must produce a variation so exceptionally stable that it constantly recurs in all the offspring of successive generations, even though those offspring are subjected to considerable change of conditions, as are the individuals of all species except the rarest or the most local. Only with such constancy and stability of inheritance could a useless character become fixed in every individual of a species, which it must be to be a "specific" character. It must, therefore, from the very first have been invariable. But this feature of invariability without selection has not been found to characterize any variation, whether occurring among wild or domesticated organisms. Such an occurrence would necessarily have forced itself upon the attention of breeders and horticulturists. For if the theory is true that the majority of specific characters are of this useless kind, their occurrence as permanent and unchangeable variations must be a common phenomenon, and we ought to find that foreign plants when first cultivated very often present new characters, not sporadically but appearing in every individual, and which cannot be got rid of, since they do not vary and selection would therefore be powerless to eliminate them. Has any indication of a phenomenon of this kind ever been noted?

Let us come now to the actual causes said to produce useless specific characters. According to Mr. Romanes they are five in number: Climate, Food, Sexual Selection, Isolation, and Laws of Growth. Let us consider how these are known to act or are alleged to act. Climate and Food undoubtedly produce modification in the individual, but it has not yet been proved that these modifications are hereditary. If this could be proved the whole discussion on the heredity of acquired characters would be settled in the affirmative. The supposed proof that these causes produce definite changes which are hereditary is derived from the fact that there is often a simultaneous change in the colours of many animals, or in the form or texture of the foliage of many plants, in different parts of the area they occupy which are characterized

by differences of climate. But in every case these changes can be interpreted as adaptations for protection in the case of the animals, and as either adaptations or individual non-hereditary modifications in the case of the plants. The firm belief that such individual characters were usually, if not always, inherited led to some looseness in Darwin's reasoning on this point, and still more so in that of most modern upholders of the theory.

The next alleged cause, Sexual Selection, whether we limit it, as I do, to the struggles of the males, leading to the development of weapons and defensive armour, or with Darwin extend it to the choice by the females of the more ornamental males, thus leading to the development of decorative plumes &c., is really a form of natural selection, and sexual characters are therefore useful characters. It is true that, from my point of view, male distinctive colour and ornament have not this particular use; and Mr. Romanes makes a good point against me when he says that in imputing their origin and development to the surplus vitality and energy of the male I give away my case, since I admit that useless specific characters may be developed independently of natural selection. This is owing to my having omitted to lay special stress on the *specific* part of each ornament being really a "recognition mark," and therefore essential both to the first production and subsequent well-being of every species. In the summary of my argument ('Darwinism,' p. 298) I have adduced the need of recognition as the cause of specific specialization of colour, but in the body of my discussion as to sexual ornaments I have not referred to it, and this omission greatly weakens my argument. I should have said that the accessory plumes and other ornaments *originate* at points of great nervous and muscular excitation, and are *developed* through surplus energy; and that, from their first appearance, they were *utilized* for purposes of recognition, which explains both their comparative stability in each species and their distinctness in allied forms*.

* Since writing this paper I have carefully studied Professor Weismann's new theory of "Germinal Selection," which seems to me to have a high degree of probability, and which, if true, enables us to explain two phenomena which have not hitherto been fully explicable. These are (1) the complete or almost complete disappearance of many characters which have become useless; and (2) the development of secondary sexual characters far beyond the point of utility as recognition marks, and, apparently, up to the extreme point of incipient hurtfulness. It thus furnishes the one link necessary in the chain of argument proving that these secondary sexual characters are explicable without calling in the very problematical agency of female choice.

The next alleged cause, Isolation, I do not admit to be a *vera causa* at all, for reasons already given. It is, at most, an aid to the differentiation of new species by natural selection.

The last alleged cause, the Laws of Growth, can never, of itself, account for specific characters, but only for those structural and histological peculiarities of organisms which characterize the higher groups such as classes and sometimes perhaps orders and families; and even these must always, when they first originated, have had a utilitarian character, since it is almost impossible to conceive that the details of structure of the various tissues or organs produced under the action of these laws were absolutely indifferent to the well-being of the organism.

If, then, we admit, as I do admit, that certain growths, appendages, or markings, which are of no use to the organism, do occasionally appear, no agency has been adduced which could, first, cause these useless characters to appear in every individual of a species, and then totally cease to appear whenever any portion of this species is selected and slightly modified so as to occupy a new place in nature or to save itself from extinction by some new enemy. Whenever useless characters are said to be "specific," it seems to be forgotten that one species has always passed continuously into another by a process of normal individual variation and survival of the fittest. There is no chasm in such a process, no sudden transition from one creature to another of a different nature. The transition is by a purely normal and almost imperceptible process of adaptation to new conditions, and in itself furnishes no reason whatever why any useless character, if it had constantly reappeared in the countless millions of individuals during all the millions of generations of the duration of the species, should at once disappear, or be replaced by some new character equally universal, equally invariable, and equally useless.

I strongly urge, therefore, that the general causes suggested by Darwin as possibly leading to the production of useless specific characters, as well as the more special causes enumerated by Mr. Romanes, do not apply to the actual facts of variation and heredity so far as they are yet known to us; and further, that no attempt has been made to show, even hypothetically, how, through the action of known causes, such characters, when they do arise, can become first extended to every individual of a species, and then be totally obliterated as regards any portion of the species which may become modified so as to constitute a new

species. Useful characters thus strictly limited are the necessary and logical results of modification through survival of the fittest. No agency has been shown to exist capable of producing useless characters similarly limited. And as it is beyond the powers of human reason to know absolutely that any characters so limited as to be really specific are and always have been useless, it is both unscientific and illogical to postulate such characters as being present in all or many species, and therefore as constituting an essential characteristic feature of specific forms.

The preceding discussion may, I hope, be considered sufficient to show that useless specific characters, if they exist, can only be the result of some comparatively rare and exceptional conditions, and that they certainly are not, as has been alleged, a general characteristic of species; but it may be as well to notice a few of the special cases which have been adduced by Mr. Romanes and others as examples of their existence or as illustrating their formation.

The Niata cattle of South America, which have strangely upturned jaws, are said to breed very true and to form a definite well-marked race which, if the character were not injurious but simply indifferent, might lead to the formation of a species defined by this useless specific character. The short-legged Ancon sheep, and the six-toed cats, are other examples of such remarkable abnormalities or sports which have the curious property of being strongly hereditary, and yet, apparently, of never leading to the formation of new species. Almost all students of evolution now admit that "sports" or large and sudden divergencies from the specific type are *not* the materials from which new species have been formed, the reason being that they are extremely rare occurrences; and when any such "sport" appeared in a species, the individual presenting it would either be avoided by its fellows and leave no offspring, or by repeated crossings with the normal type the sport would disappear. We may, no doubt, imagine conditions under which a sport of this kind, once appearing in both sexes, might lead to the formation of a breed and ultimately of a species; but the combination of conditions requisite to bring this about is so improbable that we can only look upon it as a bare possibility. But the question we are discussing is not whether, under certain very rare and exceptional conditions, a few species may possibly be formed which are distinguished only by altogether useless characters, but whether such characters are common in the

majority of species and, to use Mr. Romanes' words, exist in "enormous numbers." The case of abnormal sports or monstrosities such as those here referred to can certainly not be adduced as giving any support to this view.

The next case, that of the Porto Santo rabbits, is held by Mr. Romanes to prove that the constant characters which distinguished them from common rabbits were only results of the action of peculiar conditions on individuals, and were not produced by natural selection. He arrives at this conclusion from the fact that one of the two which died at the Zoological Gardens after four years' captivity was sent to Darwin, who found that the special colouring that distinguished the breed—the absence of black on the tail and ear-tips and the reddish colour on the back—had almost disappeared, and that the whole colouring was very little different from that of the common wild rabbit. Hence Mr. Romanes concludes that other wild species may be really only climatal forms, and their peculiar characters be non-adaptive. But no mention is made of the remarkably small size of these rabbits, which were only about half the weight of the common wild species and which looked no larger than average rats. If this also were a result of the action on the individuals of scanty food or a peculiar climate, it would have rapidly disappeared with ample food at the Zoological Gardens; and neither in this point nor in the peculiar form of the posterior end of the skull and interparietal bone, which was so distinct that Darwin figured it (see 'Animals and Plants under Domestication,' i. p. 118), did he note any difference in the dead animal. It seems probable, therefore, that the colour-peculiarities of the Porto Santo rabbits were due to a change of tint of the longer hairs which may have been lost during the illness which led to the animal's death. And as we have no information as to the supposed change having been progressive during the four years of confinement, or that it affected the second specimen, no such conclusion as that drawn by Mr. Romanes can be held to be established.

The only other case of much importance is that of changes of colour said to be directly caused by changes of climate, and especially by darkness in cave-animals. In this latter case it is declared by Mr. Romanes that the loss of colour cannot be of any use and cannot have been caused by natural selection. It is, therefore, an example of a useless character occurring in all the individuals of many unconnected species. In the case of the

Proteus, however, it is stated that when subjected to the action of light in confinement, the skin becomes dark, showing that the character is in some degree an individual one, due probably to deficiency of nutrition or, partially, to the need of light for the secretion of the pigment. The whiteness is here not a specific character. And if, in other cases, it is permanent and specific, it may have had a very obvious use in the early stages of the modification of a cave-fauna. For if any animals were isolated in caverns which were not totally dark, the light tints would be important as recognition marks, enabling the sexes to find each other; and when, at a later period, the species spread into the parts which were totally dark, there would be no cause leading to a return of the positive colour, especially as all cave-animals subjected to total darkness must at first have been in great danger of extinction from deficiency of food, and there would thus be no surplus nourishment available for the production of pigments.

Several biological friends with whom I have discussed this question, while agreeing that the majority of specific characters are useful, have suggested that useless characters may have been produced in some such manner as the following. If some useless character appears as a variation in some individuals of exceptional vigour, it may increase by interbreeding, and its repeated production being perhaps favoured by some local conditions, it may come to form a marked local variety. Now, if the conditions become unfavourable to the species in the area occupied by the type, this may in course of time become extinct, and the variety distinguished by the altogether useless character will remain as the only representative of the species. It may be admitted that such a mode of origin of a non-utilitarian specific character is conceivable, but whether it ever actually occurs in nature may be doubted; while if it does occur, it must be owing to so rare a combination of circumstances that it can produce no such general prevalence of useless specific characters as is claimed by the advocates of that theory *.

In order to ascertain whether the immediate antecedent to such a mode of species-formation as is suggested is at all common, and thinking that British flowering plants offer the best materials for its detection, I put the case to two experienced British

* If, however, the variation is preserved because it occurs in exceptionally vigorous individuals, it is correlated with a character which is useful.

botanists as follows:—Are there any examples within your knowledge of well-marked varieties (not mere individual states due to local conditions) which occupy a considerable area to the exclusion of the parent species, and which do not occupy any area, or only a very small one, with the type? Each of them suggested several species which seemed to answer to the conditions, but on further consideration it appeared that they did not do so, and we were finally reduced to a single case, that of one of the species of *Rubus*, a genus which most botanists will regard as a very unsafe one to draw any conclusions from. *Rubus radula*, Weihe, is said to be abundant in the Midland parts of England, but in the Southern and South-western counties to be replaced by the variety *anglicanus* of W. M. Rogers, the type never having been found in the area occupied by this variety. If this is the case, and the two forms, said to be easily recognizable, really occupy distinct areas and nowhere overlap, or very slightly so, then we have the condition precedent to the formation of a species by the extinction of the type, thus leaving the variety to represent the species. Of course in this case we do not know that the characters which distinguish the variety are useless; but if they are so, and if the variety should possess some superior vigour of constitution or other useful peculiarity which enables it to survive when the type dies out, we should have an illustration of one mode in which useless specific characters may possibly have arisen.

The enquiry is interesting, however, because it brings to light the rather unexpected fact, that fixed varieties of plants occupying considerable areas to the exclusion of the type are not common, and, perhaps, in our island do not exist. And should they be found to occur more frequently in other countries—as varieties of birds, mammals, and reptiles do occur in separate areas in North America—they may be usually explained as adaptations to very different climatic conditions, in which case the distinguishing characters will be utilitarian, and the local varieties will be really incipient species.

The preceding enquiry leads us to certain very definite conclusions. In the first place, we see that *species*, which have been differentiated as such by the laws of variation and survival of the fittest, must be characterized by certain peculiarities whereby they have obtained an advantage in the struggle with their fellows. These peculiarities constitute their "specific characters,"

and these *must* be useful. As this applies also to every species in the direct line of descent, the characters which are sectional or generic must also, at the time of their origin, have been useful.

In the second place, although non-utilitarian characters do undoubtedly appear in the normal course of variation, no agency has yet been detected adequate to the extension of these useless peculiarities to all the individuals which constitute a species, and, further, to prevent their extension to any of the varieties which are destined to become new species. Unless the power in question can have this twofold effect it cannot lead, except by accident, to the production of useless specific characters.

Under conceivable conditions, however, it is possible that certain useless characteristics may become limited to the individuals of a single species. But what we know of the modes of variation and the distribution of varieties indicates that, if at any time so produced, they must be altogether exceptional and of the nature of chance products; and that they cannot possibly constitute such a general characteristic of species as has been suggested.

Our final conclusion is that, whether we can discover their use or no, there is an overwhelming probability in favour of the statement that every truly *specific* character is or has been useful, or, if not itself useful, is strictly correlated with such a character.

On the Fistulose *Polymorphinæ*, and on the Genus *Ramulina*.

By T. Rupert Jones, F.R.S., and F. Chapman, A.L.S., F.R.M.S.

[Read 16th January, 1896.]

Part I.

The Fistulose Polymorphinæ.

It having been suggested that the several specimens referred to the genus *Ramulina*, Rupert Jones, may possibly belong to fistulose *Polymorphinæ*,* this memoir has been undertaken to show what evidence there is for or against the suggestion.

With this object in view, it is necessary for us to define the special *Polymorphinæ* which bear extraneous growths of fistulose form. Therefore, in the first place, we propose to take a survey of the known fistulose, tubulose, and racemose *Polymorphinæ*.

* F. B. Balkwill and F. W. Millett.—"The Foraminifera of Galway. Journ. Microsc. Nat. Sci., vol. iii. 1884, p. 33.